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Prosopagnosia does not abolish other-race effects

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ABSTRACT

Healthy observers recognize more accurately same-than other-race faces (i.e., the Same-Race Recognition Advantage - SRRA) but categorize them by race more slowly than other-race faces (i.e., the Other-Race Categorization Advantage - ORCA). Several fMRI studies reported discrepant bilateral activations in the Fusiform Face Area (FFA) and Occipital Face Area (OFA) correlating with both effects. However, due to the very nature and limits of fMRI results, whether these face-sensitive regions play an unequivocal *causal* role in those other-race effects remains to be clarified. To this aim, we tested PS, a well-studied pure case of acquired prosopagnosia with lesions encompassing the left FFA and the right OFA. PS, healthy age-matched and young adults performed two recognition and three categorization by race tasks, respectively using Western Caucasian and East Asian faces normalized for their low-level properties with and without-external features, as well as in naturalistic settings. As expected, PS was slower and less accurate than the controls. Crucially, however, the magnitudes of her SRRA and ORCA were comparable to the controls in *all* the tasks. Our data show that prosopagnosia does not abolish other-race effects, as an intact face system, the left FFA and/or right OFA are not critical for eliciting the SRRA and ORCA. Race is a strong visual and social signal that is encoded in a large neural face-sensitive network, robustly tuned for processing same-race faces.

1. Introduction

Humans are experts in recognizing faces, an ability that is critical for adapted social interactions. With a single and rapid glance at a face, we are able to extract a wide range of information, such as identity, age, physical attractiveness, gender, emotional state, or race. The processing of these biologically relevant social signals relies on the coordinated activity of an extended face cortical network (Duchaine and Yovel, 2015; Haxby et al., 2000; Ramon et al., 2015; Rossion, 2014). While some authors suggest that this network is genetically and innately organized to preferentially respond to faces (e.g., McKone et al., 2012), others posit environmental factors and experience as being critical in shaping face processing mechanisms (e.g., Arcaro et al., 2017). The other-race effect is one of the most prominent examples illustrating how experience drives face individuation and shapes our recognition abilities to be tuned to the most familiar physiognomic variations of facial morphologies present in our environment.

The other-race effect, also named same-race recognition advantage (SRRA), relates to the recognition advantage for same- (SR) compared to other-race (OR) faces. The SRRA has received extensive research attention over the last forty years. This robust effect has been observed in a wide number of behavioral studies relying on a wide range of methodologies, paradigms, databases of stimuli, and tasks involving different populations with various cultural and ethnical backgrounds (Blais et al., 2008; Golby et al., 2001; Meissner and Brigham, 2001; for a review, see, Hugenberg et al., 2010) The developmental roots of the SRRA seem to originate very early in infancy, with a preference for SR faces being observed already at 3-months of age, although the effect can be abolished at this age with an exposure to OR pictures (Anzures et al., 2010). The effect becomes more robust later in the development, at the age of 6- to 9- months. At this age, infants succeed at recognizing unfamiliar SR faces but fail with OR faces (Hayden et al., 2009; Kelly et al., 2007). The differential processing of SR and OR faces has been further observed in early and late childhood (e.g., Pezdek et al., 2003), adolescence (e.g., Goodman et al., 2007), and adulthood (e.g., Michel et al., 2006a,b; Zhao et al., 2014). In adults, the SRRA has been typically investigated with old-new tasks, first familiarizing participants with a subset of faces and then asking them to identify old *vs.* new faces within a larger set of stimuli (for a review, see, Meissner and Brigham, 2001). Interestingly some studies have shown that the SRRA can be prevented or eliminated with increasing interracial social contacts (Gajewski et al., 2008), either when participants are intentionally exposed to pictures or

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videos of OR faces (Anzures et al., 2012) or when an adoption occurs in an OR family (De Heering et al., 2010). These findings highlight the malleability of the SRRA, and show the strong influence of social exposure and face individuation in shaping face processing mechanisms, especially if social contacts occur in early childhood (McKone et al., 2019).

Another race-related effect, the other-race categorization advantage (ORCA), has also been observed in several behavioral studies. In contrast to the SRRA, whereby SR faces are better recognized than OR faces, this paradoxical phenomenon demonstrates that OR faces are more quickly and accurately categorized than SR faces (Caharel et al., 2011; Caldara et al., 2004; Contreras et al., 2013; Feng et al., 2011; Ge et al., 2009; Li et al., 2018; Liu et al., 2015; Wiese, 2013; Zhao and Bentin, 2008). Interestingly, in a behavioral study concurrently examining both the SRRA and ORCA, Ge et al. (2009) revealed a negative correlation in terms of response time between both effects. The faster observers *recognized* SR faces compared to OR faces, the slower they *categorized* SR faces as opposed to OR faces. This antagonist interaction between face *individuation* and face *categorization* is due to the very nature of face representation shaped by visual expertise underlying the same-race recognition advantage and the other-race categorization advantage (Valentine, 1991). A very high level of expertise is necessary for adequate and rapid recognition of SR faces, yet the same level of expertise negatively impacts their categorization.

One of the most prominent theoretical frameworks accounting for both other-race effects is the multidimensional face-space model proposed by Valentine (1991; see also, Valentine and Endo, 1992). According to this psychological model, faces are stored in a multidimensional space, shaped by social and visual experience. In this face space, each location represents a specific identity, and the distance from a prototypical average face is located at the center, with the multidimensional space coding for facial features and the distance between points representing the similarity between faces. Since observers are more frequently exposed to SR faces, the space dedicated to those faces results in a wider and more elaborated representations with faces being located further away from the prototypical face according to distinctive facial features shared across exemplars (i.e., color of the eyes, hair, etc. for Western Caucasian faces). However, such diagnostic information is not effective for other-race faces (for instance, all East Asian faces share dark hair and brown eyes). Fewer contacts with OR faces engender a more rudimentary multidimensional face-space, as faces are grouped together due to their high similarity. This dense cluster results in quicker categorization of OR faces as the distance is very small between the face exemplars, but slower and impaired recognition of those faces because of their lack of distinctiveness. Conversely, the high distance between SR faces leads to higher recognition judgments as face exemplars do not overlap, but slower and poorer categorization performance. This theoretical multidimensional face-space model has received support from single-cell recordings in monkeys (Leopold et al., 2006) and computational auto-associative neural networks (e.g., Caldara and Abdi, 2006).

In addition to this prominent theoretical explanation of the other-race effects, several brain imaging studies have also investigated the neural underpinnings of these perceptual phenomena. Greater neural activation to SR *vs.* OR faces have been reported in functionally defined face-selective areas of the bilateral ventral occipitotemporal cortex (VOT) during both face recognition (e.g., Golarai et al., 2020; Golby et al., 2001; Natu et al., 2011) and categorization (e.g., Feng et al., 2011; Ng et al., 2006; Wei et al., 2014) although these results are contrasted (e. g., Brosch et al., 2013; Brown et al., 2017; Contreras et al., 2013).

More specifically, an ERP study investigating the neural correlates of the SRRA with an adaptation paradigm revealed repetition suppression (RS) on the early face-sensitive N170 component only to SR, but not OR faces when the same identities were shown. These findings suggest a higher sensitivity of the face processing system to SR faces and a more efficient coding of those faces compared to OR faces (Vizioli et al., 2010). Several fMRI studies have further evidenced broader and stronger activations to the memorization and recognition of SR *vs.* OR faces in bilateral fusiform gyri, such as in the fusiform face area (FFA - Golarai et al., 2020; Golby et al., 2001; Kim et al., 2006) and ventral lateral occipital areas, where the OFA is located (Natu et al., 2011). For instance, Golby et al. (2001) conducted a fMRI study to examine the brain activity of African American, and Western Caucasian observers asked to memorize and recognize SR *vs.* OR faces with an “old-new” recognition task. Their findings reported stronger neural activations to SR *vs.* OR faces in the right FFA but not in the left FFA. Interestingly, although the authors failed to report a correlation between the neural activity in the right FFA and the magnitude of the SR recognition advantage, a positive correlation between both measures was observed in the left FFA, suggesting that this region is related to face identity memorization. More recently, in a cross-sectional study, Golarai et al. (2020) investigated the developmental time-course of the SRRA in FFAs responses in children, adolescents, and adults. Their results revealed greater recognition and stronger FFAs activation for SR *vs.* OR faces in all age groups. Their data further revealed an age-related increase in the magnitude of the SRRA in both behavioral and FFAs responses. Interestingly, the authors also reported a positive correlation between the SRRA in memory and the activity in both the left and right FFAs, suggesting that both hemispheres are involved in the development of the SRRA. Natu et al. (2011) further demonstrated that the discrimination of SR *vs.* OR faces does not depend solely on bilateral FFA activations but involves a broader range of cortical regions in the ventral temporal cortex, including ventral lateral occipital areas – where the OFA is located. Other studies, however reported more contrasted findings. For example, Kim et al. (2006) reported larger neural responses of the bilateral FFAs to SR *vs.* OR faces, yet solely when the faces were unfamiliar to the participants. More recently, Brown et al. (2017) measured overall similar SR *vs.* OR activity in the fusiform gyrus. Finally, Brosch et al. (2013) used multi-voxel pattern analysis (MVPA) to examine the blood-oxygen-level-dependent (BOLD) patterns elicited by SR *vs.* OR faces in early visual and face-selective regions. Their results revealed that the BOLD activation patterns in the early visual cortex could predict the race of the faces observed by the participants, while successful predictions in higher-face processing regions (FFA) were limited to participants with a very high implicit pro-white bias. Intriguingly, the authors did not replicate the univariate differences in FFAs activations between SR *vs.* OR faces reported in previous studies (Golarai et al., 2020; Golby et al., 2001; Natu et al., 2011). Taken together, these discrepant findings leave several issues open regarding the neural underpinnings of the SRRA. It remains to be clarified whether both bilateral FFA activations are necessary to observe this effect and what consequences damage to the left FFA, highly sensitive to memory performance, could have.

The ORCA has also been examined by several fMRI (for a review, see, Bagnis et al., 2020; Feng et al., 2011) and electrophysiological studies (e. g., Caharel et al., 2011; Caldara et al., 2004; Vizioli et al., 2010). For example, in a study by Feng et al. (2011), whole-brain analyses revealed that the categorization of SR faces elicited stronger activations in the right medial frontal cortex (rMFC) and right inferior frontal gyrus (rIFG) compared to OR faces. Regions of Interest (ROI) analyses also highlighted stronger bilateral FFAs and OFAs activations to SR *vs.* OR faces, while brain-behavior correlation analyses revealed a negative correlation between SR face categorization accuracy and left FFA activation (i. e., the higher the activity for SR *vs.* OR faces, the lower the categorization accuracy for SR faces). Finally, Psychophysiological Interaction (PPI) analyses revealed strong interactions between the posterior VOT and frontal cortical areas for SR compared to OR faces. Feng et al. (2011) concluded that more cortical resources are engaged with SR compared to OR faces due to observers’ extensive experience with those faces. Broader and stronger activations might provide more in-depth processing of SR faces (i.e., at the individual level), which might, in turn paradoxically result in slower and less accurate categorization responses of those faces at the behavioral level. Similar conclusions were drawn from an ERP study by Caldara et al. (2004), revealing that the other-race categorization advantage occurred at around 240 ms after stimulus onset in a processing stage dedicated to semantic information. The poorer experience observers have with OR faces generates fewer semantic representations, which in turn accelerates the processing speed of those faces.

To the best of our knowledge, only one study concurrently examined the neural correlates of the paradoxical behavioral effects of the SRRA and ORCA. In this study, Liu et al. (2015) asked Chinese observers to perform both face recognition and categorization by race tasks while their brain activity was monitored with fMRI. Their data showed similar bilateral FFAs', and OFAs' activations to SR faces for both tasks, while for OR faces, bilateral FFAs and OFAs activations were stronger for the recognition than the categorization by race task. These findings suggest that SR faces are deeply individuated regardless of the task at hand. In contrast, OR faces do not automatically benefit from in-depth processing, which occurs only during tasks that require face individuation. Thus, although the same neural substrates underly the processing of SR and OR faces, their activation is modulated by the race of the face, as well as individuation constraints.

To sum up, the face processing network in the ventral occipito-temporal cortex seems to be more, or at least equally activated by SR compared to OR faces, with a critical role being played by the left FFA as evidenced by significant brain-behavior correlations in this region (Feng et al., 2011; Golby et al., 2001). In fact, stronger responses in the left FFA to SR faces enhanced identity recognition performance of SR faces behaviorally (Golby et al., 2001), whereas for face categorization, the opposite pattern was true: increased activity in the left FFA impaired the categorization of SR compared to OR faces (Feng et al., 2011). While these left FFA-behavior correlational results could partially explain the trade-off relationship between the recognition of SR vs. OR faces and their categorization by race (Feng et al., 2011), further studies are necessary to provide direct proof of a causal engagement of the left FFA in both effects. Crucially, although fMRI studies can reveal correlational information between a particular task and the localization of its event in specific brain regions, this neuroimaging technique cannot unequivocally probe causal certainty about this relationship (Weber and Thompson-Schill, 2010).

To tackle this issue, brain-damaged patients can be very informative, as from their lesions and specific behavioral impairments it is possible to infer the critical role played by the damaged regions in the healthy operating system. Surprisingly, to the best of our knowledge, no study has yet investigated the other-race effects in patients with lesions to face-selective regions. To address this literature gap, here we tested PS, a well-studied pure case of acquired prosopagnosia with bilateral occipitotemporal lesions, encompassing the right OFA, the left FFA, and a small region in the right ATL. The main aim of the current study was to investigate whether face-sensitive regions play a *causal* role in both other-race effects (SRRA and ORCA). PS, healthy age-matched and young adults performed two recognition and three categorization by race tasks, with Western Caucasian and East Asian faces normalized for their frequency spectrum and contrast, with and without external features and faces presented in naturalistic settings. As expected, PS was slower and less accurate than the controls. Crucially, however, the magnitude of her SRRA and ORCA were comparable to the controls in *all* the tasks.

2. Methods

2.1. Participants

2.1.1. Patient PS's case report

Patient PS was born in 1950, she is a Caucasian case of pure acquired prosopagnosia with normal object recognition (for an exhaustive and recent review, see, Rossion, 2022a, 2022b). Her cognitive disorder resulted at the age of 42 after she underwent a closed-head injury that damaged her left mid-ventral and right inferior occipital cortex, encompassing the lFFA and rOFA respectively, as well as the right middle temporal gyrus and the left posterior cerebellum to a lesser extent (see, Sorger et al., 2007, for a precise anatomical description of her lesions). After neuropsychological rehabilitation, patient PS was able to work again as a kindergarten teacher. Despite a small left paracentral scotoma, her low-level vision is preserved with good visual acuity. Her ability to perceive and recognize objects and to discriminate faces surrounded by objects or complex scene backgrounds is within the normal range (Rossion et al., 2003a). Yet, as a consequence of her lesions, her ability to recognize the identity of faces (including the identity of her relatives and her own face) is severely impaired. She is further impaired in categorizing the gender of faces for both accuracy and sensitivity. Patient PS shows also a marked impairment in categorizing static facial expressions of emotion (Richoz et al., 2015), a deficit rooted at the level of facial information use as she directs most of her fixations toward the mouth, even when the eyes are the most informative (Fiset et al., 2017, see also, Caldara et al., 2005, for facial information use with face identity). Interestingly, PS reaches maximum recognition accuracy for all six basic expressions – except fear – when naturally evolving dynamic expressions are shown (Richoz et al., 2015). These findings reinforce the view of a distinct cortical route for the processing of dynamic face information, directly connecting early visual areas to the pSTS, a brain region anatomically spared in PS (see, Duchaine and Yovel, 2015).

2.1.2. Control participants

Two control groups took voluntarily part in our experiments. The first control group included 7 age-matched individuals from 59- to 76-years old (M = 66.9, SD = 5.6, 2 women), while the second included 46 undergraduate students (35 women) from 18- to 28-years old (M = 21.3, SD = 2.4) who obtained course credits for their participation. To avoid an effect of culture on face recognition and categorization, we ensured that all participants were Caucasian and had always been living in a Caucasian country. All participants had a normal or corrected-to-normal vision, with no neurological or psychiatric history, and were not taking any medication that could potentially slow down response time. They all took part in both experiments. Prior to the experiments, all participants signed a consent form that described the main goals of our study. The ethical committee of the department of psychology of the University of Fribourg (Switzerland) approved the study reported here.

2.2. Experiment 1 – Face recognition

We first assessed facial identity recognition accuracy of Caucasian and Asian faces with an Old-New face recognition paradigm and two different databases of stimuli: a database of Asian and Caucasian faces with external features and distinct facial expressions and a database of neutral faces without external features.

2.2.1. Materials

2.2.1.1. Stimuli with external features. We first evaluated face recognition performance using stimuli with external features (chin, outline of face, hair, ears). The stimuli were selected from the KDEF (Lundqvist et al., 1998) and AFID (Bang et al., 2001) databases and were previously used with a similar old-new face recognition paradigm in Blais et al. (2008). The stimuli consisted of 56 Caucasian (28 females) and 56 Asian identities displaying each happiness, disgust, and neutral expressions. The face pictures were black and white and placed in the middle of a grey-colored background. They did not present any distinctive features like glasses, clothes, jewelry, or scars, but the hair, chin, outline of the face, and ears were apparent. The males had all a shave. We cropped and resized the original images at the edges of the hair and neck to maintain the same visual angle across all stimuli (Fig. 1, Fig. 2). The resulting size of the images was 320 pixels in width and 361 pixels in height. They all subtended a visual angle of 14° vertically from a distance of 57 cm, corresponding to the size of a natural face during social interactions.

The stimuli were presented using the same old/new face recognition paradigm as the one used in Blais et al. (2008). More specifically, the 112 identities were divided into four blocks, two for each race (i.e., Asian and Caucasian). Each block was separated into two phases: a learning and a recognition phase. The learning phase consisted of 14 pictures (7 women), while the recognition phase consisted of the same 14 learned faces (old) and 14 new ones (Fig. 3). The identities presented in both learning and recognition phases displayed distinct expressions in each phase (e.g., disgust in the learning phase, happiness in the recognition phase). All participants saw the same stimuli in each phase, although the images were randomly presented. Each identity was assigned to only one block. The race of the first block was counterbalanced across all participants. However, after seeing one race, a block with the other race was following.

2.2.1.2. Stimuli without external features. In order to control for the impact of facial expressions and external facial features on facial identity recognition, we also evaluated face recognition performance with a database of neutral faces without external features. This methodological choice was also motivated by previous studies showing that increased attention and fixations towards internal facial features result in superior face recognition abilities (e.g., Fletcher et al., 2008, see also, Hills et al., 2014). The stimuli were selected from a database of Michel et al. (2007) and consisted of 32 Asian and 32 Caucasian faces with the same number of males and females. The differences in the stimuli number used across experiments is simply due to their availability in the face databases we took them from. The faces were presented in black and white on a grey background and were cropped at the hairline to present only the internal facial features (Fig. 4). They did not present any ornament (e.g., no glasses or jewelry) or other distinctive features (e.g., scars), and the men had a shave. We cropped and resized the original images at the chin and forehead edges to maintain the same visual angle across all stimuli. The resulting size of the images was 200 pixels in width and 252 pixels in height. They all subtended a visual angle of 14° vertically from a 57 cm-screen distance.

The 64 stimuli were separated into two blocks, one for each race. As before, each block was divided into 2 phases: a learning and a recognition phase. More specifically, for each race, 16 (8 women) faces were presented in the learning phase, and 32 (16 old and 16 new) appeared in the recognition phase. The same stimuli were presented in each phase for all participants but in random order. Note also that the facial expressions were not changing, that is the exact same faces were presented in both the learning and the recognition phase (same neutral expression).

Fig. 1. Example of a Face from the Database with External Features
Note. Example of a face (Caucasian woman expressing disgust) as it was cropped in the experiment of Blais et al. (2008) (left) and in the present experiment (right).

Importantly, we normalized all stimuli in terms of luminance, contrasts, and spatial frequency using the SHINE toolbox with the default option (Willenbockel et al., 2010). The experiment was programmed with Matlab (MATLAB, 2018) using the Psychophysics Toolbox (PTB-3; Brainard, 1997; Kleiner et al., 2007). The faces were presented on a 13-inch MacBook Pro, version 10.13.6, with a resolution of 1440 × 900 pixels and a refresh rate of 60 Hz.

2.2.2. Procedure

Participants sat 57 cm away from a computer screen in a quiet room at the University of Fribourg. They were told that they would see different blocks (learning and recognition) of faces on a computer screen, and their task would be to learn them as accurately as possible during the learning phase and recognize them among other faces during the recognition phase. After each learning phase, there was a 30s break. During the recognition phase, participants were instructed to answer as quickly and accurately as possible whether the face was familiar or not by using computer keys labeled accordingly ("S" or "L" for familiar or unfamiliar faces - counterbalanced across participants). The instructions were given by the experimenter and written on the screen. Participants were not informed about the ratio of old *vs.* new faces and no feedback was provided.

Each trial began with a black fixation cross presented for 1000 ms for the learning phase or randomly for 1000 or 2000 ms for the recognition part, to control for anticipatory strategies. The faces were presented in a random order for 3000 ms (learning phase) or until the participant responded (recognition phase) (Fig. 5). The text instructions, fixation cross, and the stimuli were all presented at the center of a grey screen.

The order of the tasks (with or without external features) was counterbalanced across participants. Participants did the whole experiment with both tasks in one session that lasted for approximately 15 min.

2.2.3. Data analysis

Data analysis was performed using RStudio 3.6.1. We merged the data of healthy age-matched (AM) and young adult (YA) control subjects as no statistically significant differences were observed between both groups. Before the analysis, we did not remove any participant for the Same-Race Recognition Advantage (SRRA) tasks, as no outlier was observed.

2.2.3.1. Recognition sensitivity. We computed d-prime (d') scores for each participant as a measure of recognition sensitivity. D-prime scores are the subtraction of the z-score for false-alarm from the z-score for hits ($d' = Z_H - Z_{FA}$). One-tailed paired-samples t-tests were computed on d' for the controls, with face race (OR (i.e., Other-Race, Asian faces) and SR (i.e., Same-Race, Caucasian faces)) as a within-subject factor for each database individually. We performed one-tailed modified t-tests, a statistical test for single case studies (Crawford and Howell, 1998), to compare the recognition sensitivity of PS with controls.

2.2.3.2. Normalized index of the SRRA. To determine the magnitude of the SRRA in identity recognition, we calculated a normalized index of the SRRA on the d'. More precisely, for each participant, we subtracted the d' for OR faces from the d' for SR faces and divided the result by the sum of the d' for SR and OR faces ($(d'_{SR} - d'_{OR})/(d'_{SR} + d'_{OR})$). Given the very nature of the present study, we decided to use the *normalized* instead of the *absolute* differences to compare the relative SR and OR face performance across participants for all the experiments. The normalization makes easy to compare the patient single case performance with those of the healthy controls. In fact, because of her brain lesions, PS is slower and less accurate than the controls and it is not straightforward to compare her performance to the heathy controls when it comes to relate a difference for two face categories (SR and OR). For example, PS

Fig. 2. Faces from the database with external features.

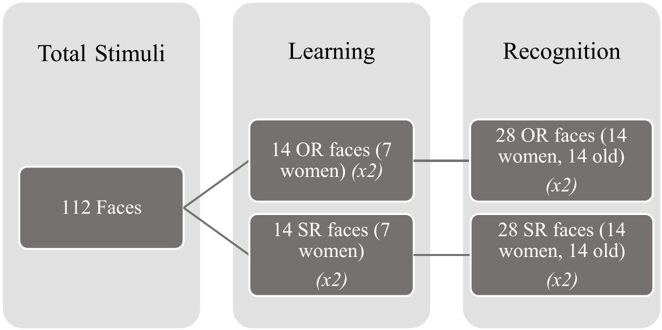

Fig. 3. Schematic Representation of the Old/New Face Recognition Paradigm
Note. A schematic representation of the old/new face recognition paradigm for the stimuli with external features. For the stimuli without external features, this procedure was repeated only once, and with 16 (instead of 14) old and new faces.

showed a difference in response time of 692 ms during the categorization by race of natural SR and OR faces. This difference in patient PS does not have the same weight or meaning than in the healthy control population, as she is globally slower to achieve natural face categorization (2313-1621 ms vs. 846-741 ms for the controls). Therefore, a normalization step is necessary to put all the participants in the same comparable scale, when computing ORE effects relating themself to a difference in performance between SR and OR faces. The obtained index value indicates the difference in recognition sensitivity between both races (i.e., the greater the index, the greater the differences in recognition sensitivity between both races). If the value of the index is positive, it indicates an advantage for SR faces (i.e., better recognition of SR faces), whereas if the value is negative, then OR faces are better recognized. We performed two-tailed modified t-tests on the SRRA index of the *d'* to compare the magnitude of the other-race effect for PS and the control participants.

Fig. 4. Faces from the database without external features.

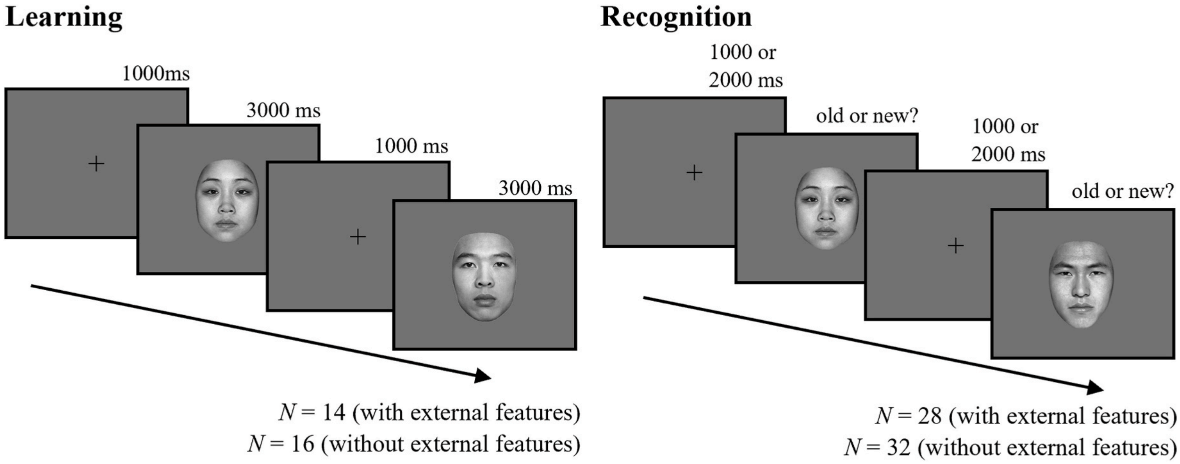

Fig. 5. The Paradigm of the Recognition Tasks
Note. Example of the procedure for the SRRA tasks (learning and recognition phases on the left and right, respectively) with the stimuli from the database without external features.

2.3. *Experiment 2 – Face categorization by race*

In Experiment 2, we assessed face categorization by race with a categorization paradigm and three different databases of stimuli. First, we used the same databases as in Experiment 1, that is stimuli with and without external features. Then, to verify if the results are generalizable to more ecological stimuli, we created a new database of faces collected from the internet (for similar stimuli, see, Rossion et al., 2015). As for Experiment 1, we normalized all stimuli for their luminance, contrasts, and spatial frequency using the SHINE toolbox with the default option (Willenbockel et al., 2010).

2.3.1. *Material*

2.3.1.1. Stimuli with external features. We used the same database of stimuli with external features as in Experiment 1. For a description of this database, see above. We used each identity only once and presented all of them with neutral facial expression.

2.3.1.2. Stimuli without external features. The same database without external features as in Experiment 1 was employed (see above). Each identity was presented once.

2.3.1.3. Natural stimuli. We created a new database of natural face pictures to assess whether the other race categorization advantage can be generalized to more ecologically valid face stimuli. We selected 36 pictures of faces with various head positions, gaze directions, age groups, contextual features (i.e., beards, scarfs, hats, glasses, clothes, or small pieces of jewelry), and natural backgrounds for each race (Asian and Caucasian) from Google images (Fig. 6).

More precisely, for each ethnical group, we selected a similar number of men and women ($N = 18$), front and side faces (N = 19), and faces with the gaze directed away and towards the participant ($N = 19$). We also controlled for the backgrounds of the pictures (plain, with clear or blurred details), the age groups, the facial expressions (13 slightly smiling and 23 neutral faces), and facial attractiveness to ensure that all these characteristics were similar in both groups. To control for the positions of the internal facial features (i.e., eyes, noses, mouths), we used Matlab (MATLAB, 2018) to draw a triangle from the outer ends of the eyebrows to the upper two-thirds of the chin of each face (Fig. 7a). We then summed the position of the different triangles, which showed a similar pattern of face positions in both ethnical groups (Fig. 7b). All faces were presented with their background and were 200 × 200 pixels. They all subtended a visual angle of 14° vertically from a viewing distance of 57 cm. Each identity was presented once.

We again used a 13-inch MacBook Pro, version 10.13.6, with a resolution of 1440 × 900 pixels and a refresh rate of 60 Hz for the three categorization by race tasks. The tasks were also launched with the use of Matlab (MATLAB, 2018) and its Psychophysics Toolbox (PTB-3; Brainard, 1997; Kleiner et al., 2007).

2.3.2. *Procedure*

Upon their arrival, participants sat 57 cm away from a computer screen in a quiet room at the University of Fribourg. They were told that

Fig. 6. Example of faces from the natural database.

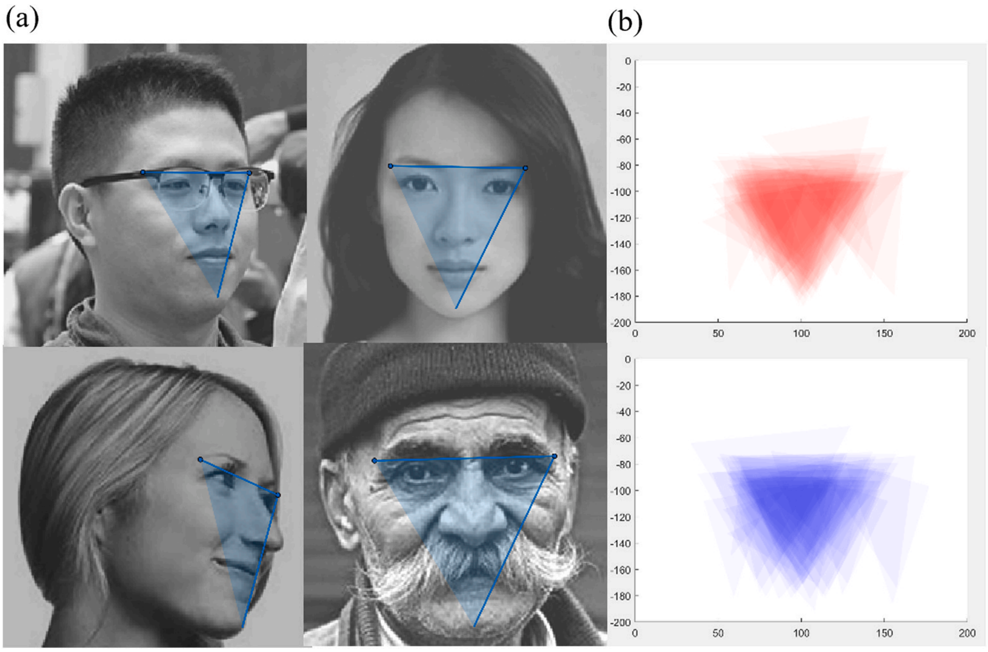

Fig. 7. Example of Control of Internal Features Positions
Note. (a) Example of internal facial feature positions for two Asian (top) and two Caucasian (bottom) faces in front (center) or side view (left) view and (b) the summation of the internal features for all faces of each race (Asian and Caucasian in red and blue, respectively).

faces would be presented on the screen and that they would have to categorize each one according to its race (i.e., "Asian" or "Caucasian") as quickly and accurately as possible by using the labeled computer keys ("s" or "l" – semi-randomized across participants). The instructions were orally explained by the experimenter and repeated on the screen at the beginning of the experiment. The ratio of faces from both races was not told to the participants, and they did not receive any feedback.

Each trial began with a fixation cross presented for a random duration of 1000 or 2000 ms to control for anticipatory strategies (Fig. 8). A randomly chosen face then appeared on the screen until the participant answered. All faces of each database were presented, and each face was presented only once. The instructions, fixation cross, and the stimuli were all presented in the center of the screen on a grey background. All texts were written in black.

The order of the tasks (with or without external features or natural stimuli) was semi-randomized across participants. They participated in the four categorization tasks in one session, which lasted for approximately 25 min.

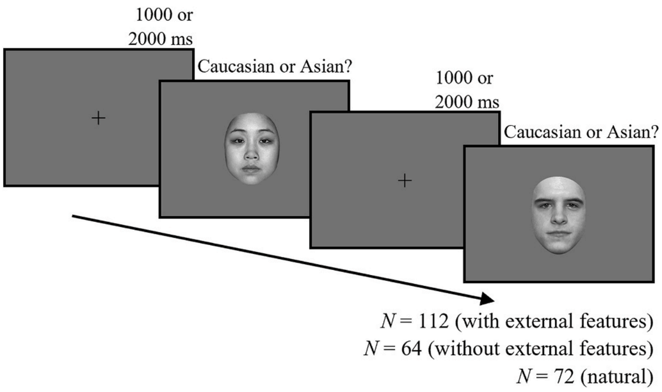

Fig. 8. The Paradigm of the Categorization Tasks
Note. Example of the procedure for the categorization by race tasks with the stimuli from the database without external features.

2.3.3. Data analysis

As for the recognition tasks, data analysis was performed with the use of RStudio 3.6.1. And as no statistical difference was found between the performances of the AM and YA controls, we merged their data. For the Other-Race Categorization Advantage (ORCA) tasks, we only considered the trials with correct responses in our analyses and from those trials excluded one AM participant as his mean response time was considered as an extreme outlier compared to the other AM participants.

2.3.3.1. Response time. For the ORCA tasks, only the response times for correct answers were taken into account in the analyses. For the controls, we performed one-tailed paired-samples t-tests on the response time (RT) with the race of the faces (OR and SR) as a within-subject factor. We further performed one-tailed modified t-tests to compare the differences in accuracy and response time between PS and the controls.

2.3.3.2. Normalized index of the ORCA. To determine the magnitude of the ORCA, we computed a normalized index with the RT obtained for each race. More precisely, for each participant, we subtracted the RT for OR faces from the RT for SR faces and divided the result by the sum of the RTs for SR and OR faces (i.e., $(RT_{SR} - RT_{OR})/(RT_{SR} + RT_{OR})$. We performed two-tailed modified t-tests on the ORCA index to compare the magnitude of the ORCA between PS and the controls.

3. Results

3.1. Experiment 1 – Face recognition

3.1.1. Recognition sensitivity

3.1.1.1. With external features. For controls, one-tailed paired-samples t-tests revealed a significant main effect of race for the database with external features, $t\ (52) = 11.35$, $p < .00$, $d = 1.56$, 95% CI [0.53, ∞] (bracket shows the lower and upper limits of the 95% confidence interval). Participants had a higher recognition sensitivity for SR ($M = 1.4$, $SD = 0.4$) than OR ($M = 0.7$, $SD = 0.4$) faces.

For PS, one-tailed modified t-tests indicated that she had a significantly lower recognition sensitivity than 94.2% of the controls for SR faces ($M = 0.5$), and that this difference was significant, $t\,(52) = -1.94$, $p = .03$ (Fig. 9, Fig. 10, see also, supplementary results, Table S1). For OR faces, PS had lower *d'* ($M = 0.3$) than 70.9% of the controls, but this difference was not significant, $t\,(52) = -1.07$, $p = .15$. Bêta scores and confusion matrices are also reported separately in the Supplementary Fig. S1 and Supplementary Fig. S2, respectively.

3.1.1.2. Without external features. One-tailed paired-samples t-tests also indicated a significant main effect of race for the database without external features for the controls, $t\,(52) = 11$, $p < .00$, $d = 1.51$, 95% CI [0.73, ∞]. Participants were better at recognizing SR ($M = 1.5$, $SD = 0.6$) than OR ($M = 0.6$, $SD = 0.5$) faces.

Although PS was lower than 84.1% of the controls for SR faces ($M = 0.7$), the one-tailed modified t-tests indicated that this difference was only marginally significant, $t\,(52) = -1.43$, $p = .08$ (Figs. 9 and 10, see also, supplementary results, Table S1). PS had lower sensitivity than 61.8% of the controls for OR faces ($M = 0.2$), but the difference was not statistically different, $t\,(52) = -0.88$, $p = .19$. Bêta scores and confusion matrices are also reported separately in the Supplementary Fig. S1 and Supplementary Fig. S2, respectively.

3.1.2. Normalized index of the SRRA

3.1.2.1. With external features. According to the two-tailed modified t-tests, the magnitude of the same-race recognition advantage on the *d'* for faces with external features was similar for PS ($M = 0.29$) and the controls ($M = 0.34$, $SD = 0.27$), $t\,(52) = -0.18$, $p = .86$ (Fig. 11, see also, supplementary results, Table S3).

3.1.2.2. Without external features. Similarly, for faces without external features, the magnitude of the same-race recognition advantage on the recognition sensitivity was not significantly different for PS ($M = 0.6$) and the controls ($M = 0.49$, $SD = 0.39$), $t\,(52) = 0.28$, $p = .78$ (Fig. 11, see also, supplementary results, Table S3).

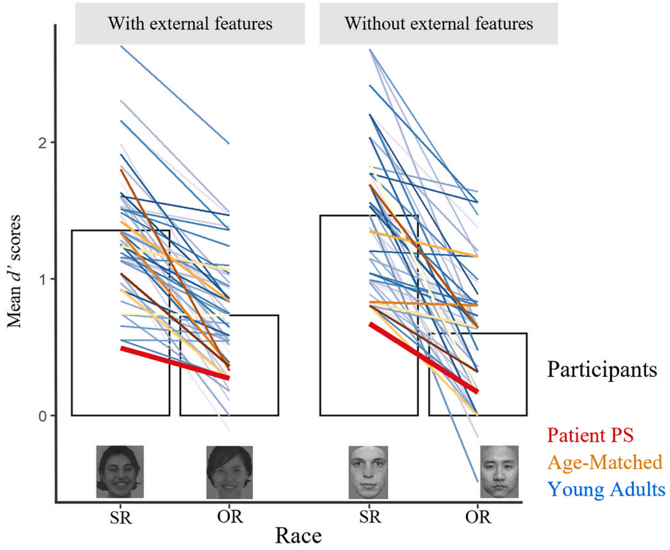

Fig. 9. Mean d' for the SRRA Tasks
Note. Mean *d'* for each group of participants (YA, AM, and PS, in blue, orange and red, respectively) according to each race (SR and OR) in each database (with and without external features, on the left and right, respectively).

3.2. Experiment 2 – Face categorization by race

3.2.1. Response time

3.2.1.1. With external features. All participants were highly accurate for the ORCA task, whether they had to categorize OR ($M_{PS} = 86\%$, $M_{Controls} = 98\%$, $SD_{Controls} = 4\%$) or SR ($M_{PS} = 90\%$, $M_{Controls} = 98\%$, $SD_{Controls} = 3\%$) faces with external features. PS was however significantly less accurate than more than 99% of the controls for both OR $t\,(51) = -2.9$, $p = .003$, and SR faces, $t\,(51) = -3.31$, $p = .001$, respectively, as highlighted by the one-tailed modified t-tests.

For the response times, the one-tailed paired-samples t-tests indicated that the control participants were faster to categorize OR ($M = 681.4$ ms, $SD = 130.8$) than SR ($M = 710.9$ ms, $SD = 135.1$) faces, $t\,(51) = 2.58$, $p = .006$, $d = 0.36$, 95% CI [10.35, ∞].

Compared to the controls, the one-tailed modified t-tests indicated that PS was slower than 93.5% of the controls for OR faces ($M = 930.5$ ms, $SD = 282.1$) and 99.2% of the controls for SR ones ($M = 1086$ ms, $SD = 236.9$) (Fig. 12, see also, supplementary results, Table S2). Both differences were statistically significant, $t\,(51) = 1.89$, $p = .032$, and, $t\,(51) = 2.75$, $p = .004$, for OR and SR faces, respectively.

3.2.1.2. Without external features. For the faces without external features, the categorization performance of the controls were also high for both OR ($M_{PS} = 94\%$, $M_{Controls} = 98\%$, $SD_{Controls} = 3\%$) and SR ($M_{PS} = 88\%$, $M_{Controls} = 97\%$, $SD_{Controls} = 4\%$) faces. The one-tailed modified t-tests indicated that PS was different from only 81.7% of the controls for OR ones, $t\,(51) = -1.35$, $p = .09$, but had a significantly lower accuracy than 98.8% of the controls for SR faces, $t\,(51) = -2.61$, $p = .006$.

One-tailed paired-samples t-tests further revealed that the controls categorized OR faces ($M = 684.8$ ms, $SD = 137.2$) faster than SR ones ($M = 792.9$ ms, $SD = 208.3$), $t\,(51) = 6.06$, $p < .00$, $d = 0.84$, 95% CI [78.27, ∞].

For PS, one-tailed modified t-tests showed that she was significantly slower than 99.8% of the controls for OR faces ($M_{OR} = 1131.2$ ms, $SD_{OR} = 309.6$), $t\,(51) = 3.22$, $p = .001$, as well as 91.4% of the controls for SR faces ($M_{SR} = 1161.3$ ms, $SD_{SR} = 327.7$), $t\,(51) = 1.75$, $p = .043$ (Fig. 12, see also, supplementary results, Table S2).

3.2.1.3. Natural. In a more natural context, the control participants were also highly accurate to categorize OR ($M_{Controls} = 97\%$, $SD_{Controls} = 3\%$) and SR ($M_{Controls} = 97\%$, $SD_{Controls} = 3\%$) faces by race. The one-tailed modified t-tests indicated that PS was however less accurate than 100% of the controls for both OR ($M = 75\%$) and SR ($M = 81\%$) faces, $t\,(51) = -6.44$, $p < .001$, and, $t\,(51) = -5.32$, $p < .001$, respectively.

As indicated by the paired-samples t-tests, the controls were also faster to categorize OR ($M = 752.1$ ms, $SD = 148.7$) than SR ($M = 859.1$ ms, $SD = 229.5$) individuals, $t\,(51) = 4.84$, $p < .00$, $d = 0.67$, 95% CI [69.93, ∞].

For PS, one-tailed modified t-tests further revealed that she was significantly slower from 100% of the controls for both OR ($M = 1621.9$ ms, $SD = 647.5$) and SR ($M = 2313.8$ ms, $SD = 971.6$) faces from the natural database (Fig. 12, see also, supplementary results, Table S2). Her scores are significantly different from the control participants, $t\,(51) = 5.79$, $p < .001$, and, $t\,(51) = 6.28$, $p < .001$, for OR and SR faces, respectively.

3.2.2. Normalized index of the ORCA

3.2.2.1. With external features. The magnitude of the other-race effect on the RT was similar for PS ($M = 0.08$) and the controls ($M = 0.02$, $SD = 0.05$) for the database with external features, $t\,(51) = 1.06$, $p = .3$ (Fig. 13, see also, supplementary results, Table S3).

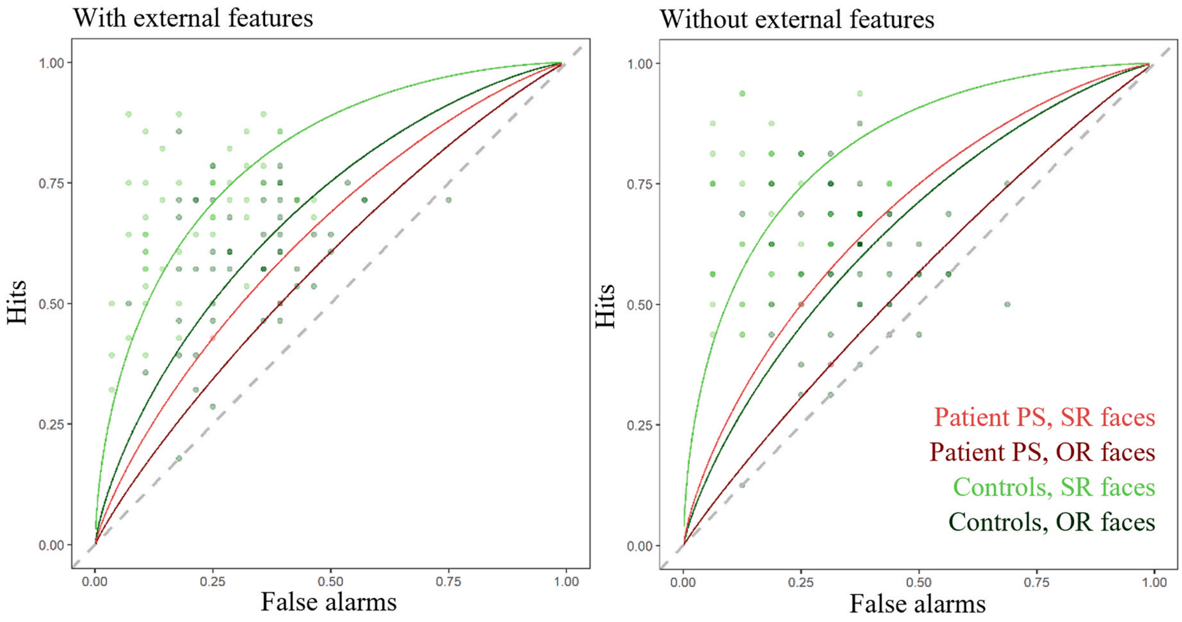

Fig. 10. ROC Curves
Note. ROC curves for PS and the controls (in red and green, respectively), for the OR and SR faces (darker and lighter curves, respectively) with or without external features (left and right, respectively).

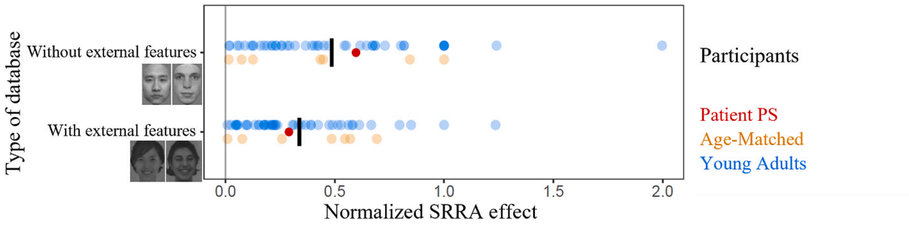

Fig. 11. Normalized SRRA index on the d'
Note. Normalized SRRA index on the *d'* for each type of participant (YA, AM, and PS, in blue, orange and red, respectively) according to the type of database (with or without external features, up and below, respectively). Values on the right side of the graph indicates greater SRRA, that is, better recognition of SR than OR faces.

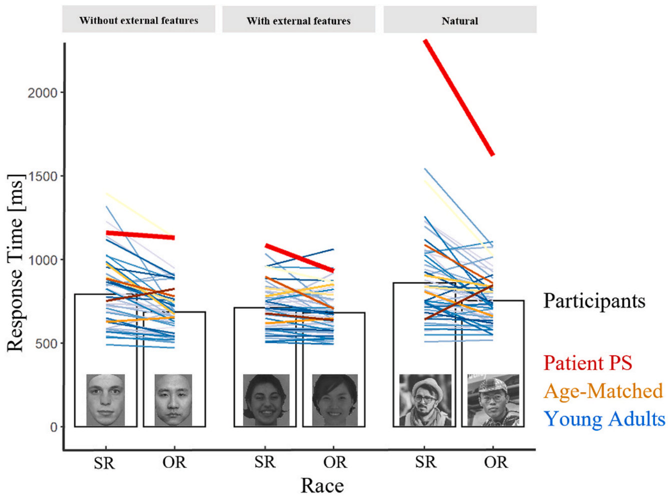

Fig. 12. Mean Response Time for the ORCA Tasks
Note. Mean response time for each group of participants (YA, AM, and PS, in blue, orange and red, respectively) according to each race (SR and OR) in each database (without, with external features, and natural, from the left to the right, respectively).

3.2.2.2. Without external features. Similarly, for the faces without external features, the magnitude of the ORCA of PS ($M = 0.01$) was not significantly different from the controls ($M = 0.07$, $SD = 0.07$), $t\ (51) = -0.75$, $p = .46$ (Fig. 13, see also, supplementary results, Table S3).

3.2.2.3. Natural. Finally, with natural faces, the magnitude of the ORCA was similar between PS ($M = 0.18$) and the controls ($M = 0.06$, $SD = 0.08$), $t\ (51) = 1.37$, $p = .18$ (Fig. 13, see also, supplementary results, Table S3).

4. Discussion

The present study examined *whether* and *how* acquired prosopagnosia modulates the same-race recognition advantage (SRRA) and the other-race categorization advantage (ORCA) to shed further light on the neural substrates underlying both effects. Several brain imaging studies previously reported the FFA and OFA as key regions for processing race in faces. Yet, it remained to be clarified whether these brain regions play a *causal* role in those other-race effects. To this aim, we tested patient PS, a pure case of acquired prosopagnosia with occipito-temporal lesions to the right OFA, the left FFA, and a small part of the right anterior temporal lobe. We first assessed patient PS and healthy controls' ability to recognize SR and OR faces with the use of old-new tasks and then examined their response time when asked to categorize SR and OR faces by race. To assess both other-race effects in patient PS, we computed the magnitudes of the SRRA and ORCA in our healthy

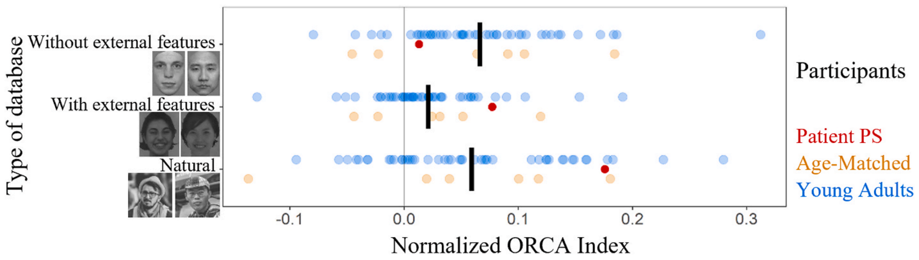

Fig. 13. Normalized ORCA Index on the Response Time

Note. Normalized ORCA index on the response time for each type of participant (YA, AM, and PS, in blue, orange and red, respectively) according to the type of database (without, with external features and natural, from top to bottom, respectively). Values on the right side of the graph indicates greater ORCA, that is, quicker categorization of OR than SR faces.

controls and compared the obtained results to the magnitudes of the effects observed in patient PS.

As predicted, our findings revealed the typical behavioral other-race effects in face recognition and categorization by race in our healthy controls. Our participants were more accurate at recognizing SR than OR faces, but categorized OR faces more rapidly than SR ones, replicating the previously found other-race effects in memory (e.g., for reviews, see, Hugenberg et al., 2010; Lee et al., 2011; Meissner and Brigham, 2001) and categorization (Caharel et al., 2011; Caldara et al., 2004; Contreras et al., 2013; Feng et al., 2011; Ge et al., 2009; Li et al., 2018; Liu et al., 2015; Wiese, 2013; Zhao and Bentin, 2008), thus corroborating the face-space model predictions (Valentine, 1991).

Without surprise, our results further revealed that PS was significantly less accurate in recognizing SR but not OR faces and slower in categorizing both SR and OR faces relative to healthy controls. These results are consistent with her prosopagnosia (Rossion et al., 2003a; Schiltz et al., 2006) and align with the idea that lesions to the FFA and/or OFA affect SR face processing abilities (Dalrymple et al., 2011; Pitcher et al., 2007; Rossion et al., 2003a,b; Steeves et al., 2006). However, the comparison of PS' performance for both races in the recognition and categorization tasks might seem discrepant at first sight. Her lesions seem to affect both SR and OR faces in the categorization tasks, but SR faces solely for the recognition tasks. In fact, PS and the healthy controls were equally impaired during OR face recognition. This observation is fully in line with a recent study showing that a higher rate of individuals meet the clinical criteria of *face-blind* when recognition is tested with OR compared to SR faces (Wan et al., 2017). We observed very similar results to those reported by Wan et al. (2017), as a high rate of healthy controls poorly performed during the OR face recognition tasks in our study. This resulted in a non-significant difference between PS and the healthy controls for OR face recognition. Interestingly, however, the novelty of our work lies in the magnitudes of the other-race effects observed for PS, as they were in the range of the healthy controls despite her functional impairment and brain lesions. These data provide unequivocal evidence that acquired prosopagnosia does not abolish the other-race effects, and overall support the claim that an intact face cortical network - with undamaged FFA and/or OFA - is not necessary to observe these effects. These observations suggest that a common mechanism outside those areas is impaired in processing OR compared to SR faces in both PS and healthy observers.

4.1. An intact face cortical network is not necessary to observe the other-race effects

Despite extensive lesions encompassing the right OFA and the left FFA, the magnitudes of the SRRA and ORCA of patient PS are within the range of controls. These results question the interpretation of previously reported brain imaging findings that have pointed towards the involvement of these brain regions in the SRRA and ORCA. For example, several studies have consistently reported greater activation of the bilateral FFA and OFA when viewing SR than OR faces, whether the participants were asked to recognize (Golarai et al., 2020; Golby et al., 2001; Kim et al., 2006) or categorize faces (Feng et al., 2011), and in both Caucasian (Golarai et al., 2020; Golby et al., 2001) and Asian participants (Feng et al., 2011; Kim et al., 2006). These results suggest that the activity of the FFA and OFA is modulated by the perceived race. In addition, previous work also reported brain-behavior correlations between the other-race effects and the left FFA (Feng et al., 2011; Golarai et al., 2020; Golby et al., 2001), with larger activation for SR faces being associated with greater SR face recognition performance but worst categorization abilities. Since strong correlations between behavioral performance and the activations of the FFA and/or OFA have often been reported, one might posit that these face-selective areas are causally engaged in the other-race effects. However, here, for the first time, we demonstrate that the lFFA and/or the rOFA are not causally necessary to observe the SRRA and the ORCA, at least not in a *qualitative* (i.e., absolute) manner, as PS showed comparable magnitudes of other-race effects as controls. Rather, our data suggest that an intact face-sensitive neural network plays a *quantitative* role in face recognition and categorization by race by boosting the accuracy and speed of behavioral performance. Future studies are necessary to directly examine the specific mechanisms played by the FFA and the OFA that enhance face recognition performance in the other-race effects.

4.2. An extended and robust neural network supports race processing from faces

Our study reinforces previous evidence suggesting that the processing of face race does not solely depend on the FFA and OFA but involves an extended race-sensitive network that goes well beyond occipito-temporal areas. For instance, previous work reported distinct activations for SR relative to OR faces in frontal regions, such as in the right medial frontal cortex (rMFC) (Feng et al., 2011), the inferior frontal gyrus (IFG) (Feng et al., 2011; Greer et al., 2012), the dorsolateral prefrontal cortex (DLPFC) (Cunningham et al., 2004; Richeson et al., 2003) or the anterior cingulate cortex (ACC) (Cunningham et al., 2004; Greer et al., 2012; Richeson et al., 2003). More posterior areas have also been reported to be involved in race processing, with greater SRRA-related functional connectivity between the fusiform cortex and the medial intraparietal sulcus and distinct activations for SR relative to OR faces in frontoparietal areas (Brown et al., 2017) or in the right STS (Earls et al., 2013; Liu et al., 2015). Natu et al. (2011) demonstrated that a large spatial map in the VT cortex extending to the fusiform gyrus and ventral lateral occipital areas was involved in dissociating SR and OR faces. Components of the limbic system also demonstrated stronger activations in response to SR relative to OR faces. Such results were observed for the amygdala (Cunningham et al., 2004; McCutcheon et al., 2018; Phelps et al., 2000; Platek and Krill, 2009, but see also, Lieberman et al., 2005), hippocampal and parahippocampal areas (Cunningham et al., 2004; Greer et al., 2012) whose activations were also correlated with the SRRA (Golby et al., 2001). As these above-mentioned frontal, frontoparietal and limbic regions are involved in high-level processes, such as conflict resolution, inhibition, memory, social, cognitive, or emotional control, among others, their recruitment in race processing is likely a demonstration of the involvement of top-down processes in the perception of face race. Finally, some studies also reported successful race prediction from the activity in the primary visual cortex (Brosch et al., 2013; Kaul et al., 2014; Ratner et al., 2013). However, the stimuli used in these studies radically differed in terms of low-level features (e.g., skin color). Consequently, the differential activations observed in the primary visual cortex in response to faces of different races might solely mirror an efficient coding of low-level visual components.

To sum up, in addition to the FFA and OFA, previous studies have reported that a large number of frontal, frontoparietal, and limbic regions are involved in race processing. These areas are intact in patient PS (Sorger et al., 2007) and might have been recruited to efficiently process facial race. In line with previous studies, our findings provide further evidence that facial race is subtended by an extensive network involving regions that are not exclusively dedicated to the processing of faces. Future neuroimaging studies with PS are necessary to precisely map out the brain regions dedicated to the processing of SR and OR faces in the absence of the lFFA and rOFA during face recognition and categorization by race. This would further sharpen our understanding of the brain regions engaged in these paradoxical other-race phenomena.

4.3. Early tuning to same-race faces

The other-race effects seem to originate very early in infancy with a behavioral SRRA observed as soon as 3-months of age (Anzures et al., 2010; Hayden et al., 2009; Kelly et al., 2007, 2009). As early as 7 months of age, the eye movements of infants are also tuned to distinct cultural facial features to process facial expressions of emotion in Western and Eastern infants (Geangu et al., 2016). The neural substrates of race processing undergo changes throughout development and tune to SR faces with age. For instance, the FFA (Golarai et al., 2020), IFG (Ding et al., 2014), right middle frontal gyrus (Ding et al., 2014), and left cuneus (Ding et al., 2014) experience developmental changes across age in response to race. Note that some of these areas were also identified as race-sensitive in adults in the previously mentioned studies of Feng et al. (2011) or Greer et al. (2012). Previous studies also reported that the functional connectivity within occipital areas and between occipital and frontal areas strengthens with age for both SR and OR faces (Ding et al., 2014; Zhou et al., 2016). Finally, Telzer et al. (2013) noticed that early deprivation to OR faces was associated with enhanced amygdala activations for OR faces. These findings highlight an early tuning in the face system to race with connectivity with other brain regions changing and strengthening with experience. PS might still also benefit from this early tuning towards same-race faces, as the magnitude of her SRRA and ORCA are comparable to the controls. This observation, coupled with previous neuroimaging evidence in healthy adults, posits the view that race is a strong visual and social feature that is encoded in an extensive brain network, going well beyond the face-sensitive regions.

In general, our results also invite to caution when interpreting neuroimaging results and drawing conclusions on the functional involvement of brain regions in cognitive tasks acquired on the sole adult healthy population. Corroborative complementary *causal* Transcranial Magnetic Stimulation (TMS) and patient studies are necessary to draw solid functional theories.

5. Conclusions

Understanding the neural substrates of race processing is of societal importance, as these biological social cues are automatically processed and influence our everyday interactions and behaviors. Our results confirm previous observations that individuals are markedly impaired in processing other-race faces while categorizing them by race faster than same-race faces. We critically provide novel evidence that prosopagnosia does not abolish the other-race effects. Our results reveal indeed that lesions in face-selective areas, specifically the lFFA and/or the rOFA, are not critical to observe the SRRA and ORCA, since PS's lesions on those brain areas do not prevent the patient from showing an advantage comparable to the healthy controls for both other-race effects. Other areas responding to race, such as frontal, frontoparietal, or limbic regions, may have been recruited in patient PS to show similar sensitivity to face race. Race seems, therefore, to be encoded in a large face-sensitive network, going well beyond the face network in the ventral occipitotemporal cortex. The biological and social importance of the race signal might also be rooted in the brain by an early developmental tuning to familiar same-race faces. Altogether, our results provide novel insights into the neuroanatomy of the other-race effects and reveal one of the rare, preserved face-related sensitivity in the prosopagnosic patient. But more importantly, they go well beyond the field of face perception, as they invite to caution when interpreting neuroimaging results and drawing conclusions on the sole correlational involvement of brain regions in cognitive tasks acquired in the healthy adult population. Confirmatory causal studies as the present study are necessary for this scope.

Credit author statement

Pauline Schaller: Methodology, Software, Validation, Formal Analysis, Investigation, Writing-Original draft preparation, Writing-Reviewing and Editing, Visualization, Project administration. Roberto Caldara: Conceptualization, Resources, Writing-Reviewing and Editing, Supervision, Funding acquisition. Anne-Raphaëlle Richoz: Writing-Reviewing and Editing, Supervision, Project administration.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

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Appendix 2. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108479.

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